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Potential Interference Between a Threatened Endemic Thistle and an Invasive Nonnative Plant

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Abstract: *Although the establishment of nonnative plants is recognized as a threat to native ecosystems, there are few documented examples of an invasive species directly influencing a rare native plant. The Eurasian biennial* Dipsacus sylvestris *(teasel) is invading the central New Mexico habitat of* Cirsium vinaceum, *an endemic thistle that is federally listed as threatened. We documented changes in teasel distribution and abundance between 1989 and 1993 that suggest the potential for direct interactions with the native thistle. We then compared habitat characteristics, germination behavior, and performance in greenhouse and field competition trials to evaluate the potential outcome of interference between these two species. There were no significant differences in measured habitat characteristics between sites supporting* C. vinaceum *and those with* D. sylvestris. Dipsacus *was better able to germinate in low light than the thistle, suggesting that* D. sylvestris *might invade* C. vinaceum *populations but that thistle recruitment would be unlikely in dense stands of the nonnative plants. In the greenhouse growth of* C. vinaceum *rosettes was significantly reduced by the presence of* Dipsacus, *but the invader was unaffected by the thistle; results of a short-term field experiment were equivocal but suggestive of interference between the two. We suggest criteria for managers to use in determining whether invading species pose problems for specific rare native taxa, and we discuss the constraints on experimental work where protected taxa are involved.*

Interferencia potencial entre un cardo endémico en peligro y una planta invasora no nativa

Resumen: *Si bien el establecimiento de plantas no nativas es reconocido como una amenaza para los ecosistemas nativos, hay pocos ejemplos documentados de una especie invasora que afecte directamente a una planta nativa rara. La planta bianual Eurasiática* Dipsacus sylvestris *(carda) esta invadiendo el hábitat de una especie amenazada, Cirsium vinaceum, en el centro de Nuevo México (EEUU). Documentamos cambios en la distribución y abundancia de carda entre 1989 y 1993 que sugieren la posibilidad de interacciones directas con el cardo nativo. Comparamos luego las características del hábitat, el comportamiento germinativo y el desempeño en experimentos de competición en invernaderos y en viveros a efecto de evaluar el resultado posible de la interferencia entre estas dos especies. No existieron diferencias significativas entre las características del hábitat registaradas en sitios que mantenian* C. vinaceum *y aquellos con* D. sylvestris. Dispsacus *fue más apto para germinar bajo poca luz que el cardo, lo que sugiere que* D. sylvestris *podría invadir poblaciones de* C. vinaceum *y que el reclutamiento del cardo seria poco probable en parcelas densos de la planta no nativa. En el invernadero el crecimiento de las rosetas de* C. vinaceum *fue reducido significativamente por la presencia de* Dipsacus, *pero la planta invasora no fue afectada por el cardo; los resultados del experimento a corto plazo en el vivero fueron ambiguos pero sugieren la existencia de interferencia entre estas dos especies. Sugerimos criterios a ser usados por los administradores para determinar si una especie invasora plantea problemas para un taxón nativo raro en particular y discutimos las limitaciones del trabajo experimental que involucra taxones protegidos.*

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Introduction

Conservation of native plants or plant communities has sometimes been viewed simplistically as the identification of critical areas and their protection from further direct human disturbance (land clearing, vehicle impacts, etc.). But even seemingly undisturbed habitats have experienced substantial changes from presettlement conditions: fragmentation, isolation from other areas with similar habitat, alterations of disturbance regime, or changes in climate or nutrient inputs. One of the most important of these changes is the introduction of new species, some of which become invasive or successful in native ecosystems (Coblentz 1990; Soulé 1990).

It is recognized that invasive plants may present significant problems for the conservation of natural areas by exerting any of several system-level effects (Vitousek 1986; Ramakrishnan & Vitousek 1989; Hobbs & Huenneke 1992). The establishment of some plant species may alter the disturbance regime on a site, thereby suppressing or eliminating native species; for example, in many parts of the world, introduction of productive, fire-tolerant grasses has led to an increase in the frequency of hot fires, which has in turn damaged or eliminated fire-sensitive native plants (see Hughes et al. 1991; D'Antonio & Vitousek 1992). Other invasive plant species can alter nutrient and hydrological cycles within an ecosystem. In Hawaii, the invasion of a nonnative nitrogen fixing tree has increased the rate of nitrogen accumulation in post-volcanic successions, with possible consequences for altering the natural successional sequence (Vitousek et al. 1987; Vitousek & Walker 1989). In the American Southwest, the establishment of *Tamarix* spp. has drawn down the water table in many riparian and wetland sites, even drying up some desert springs completely, thus removing the conditions necessary for native wetland vegetation (Horton 1977).

Another potential result of invasion is the direct competitive displacement of native species, particularly those whose numbers are few or whose biological status is threatened. When a novel species enters a community and becomes abundant, the result may be the direct shading of natives, competition for soil resources or for pollinators, alteration of soil surface conditions necessary for germination, or allelopathic effects, any of which might decrease the abundance or continued persistence of native plants. Several studies have documented competition for water between nonnative plants and native species, with the consequent reduced performance of the native plants (see Danielsen & Halvorson 1991; D'Antonio & Mahall 1991; Elliott & White 1987; Melgoza et al. 1990; Weiss & Noble 1984). Obtaining a detailed understanding of competitive interactions among species requires careful experimentation and physiological work, either in greenhouse, growth chamber, or (preferably) the field.

There are cases where the decline or vulnerability of a rare species has been attributed to the negative effects of nonnative plant competitors (see *Amsinckia grandiflora* in California grassland dominated by nonnative annuals; Pavlik 1990). Few published cases, however, clearly demonstrate the threat of particular invaders to specific conservation targets. This lack of examples may deter some managers from the aggressive, expensive control programs necessary to limit the spread and effect of nonnative plants. The absence of documentation undoubtedly is partly due to the difficulty of performing careful experimentation on rare or protected species.

Ideally, managers or conservationists would like to evaluate potential conflicts between particular invaders and particular natives, especially rare or sensitive species, in time to allow preventive action before the situation reaches a critical stage. If managers wait to act until the deleterious effects of invasion are clearly evident (in decreased populations of the rare native, for example), control actions will be much more difficult and expensive. We present here a case study of the encroachment of an aggressive invader, teasel (*Dipsacus sylvestris* [Dipsacaceae]), in the habitat of a federally threatened endemic plant, Sacramento Mountains or Mescalero thistle (*Cirsium vinaceum* [Woot. & Standl.]). After documenting that the teasel is moving into the rare thistle's habitat, we apply several methods of assessing potential interference or competition, and we discuss constraints on their use where protected species or sites are involved.

Cirsium vinaceum is a narrow endemic restricted to the cool, moist refuge provided by the Sacramento Mountains in the northern Chihuahuan Desert. It is a large, robust member of the Compositae; rosettes spend one to several years in a vegetative stage before flowering once and dying, but multiple rosettes may be produced by a single plant (Thomson 1991). The thistle is restricted to springs, seeps, and streamsides in certain watercourses of the Sacramento Mountains, largely within the Lincoln National Forest. Plants are distributed in clusters or dense stands that may be separated from one another by 50 to hundreds or meters or more within a given watercourse. Due to its narrow endemism and its dependence on water sources that are facing pressure from development and other uses, *C. vinaceum* was listed as a threatened species under the Endangered Species Act in 1987 (U.S. Fish and Wildlife Service 1987, 1993).

Dipsacus sylvestris is a native of Europe that has become a ubiquitous weed in much of the United States. Teasel has recently become established in some New Mexico montane watercourses, including some *Cirsium vinaceum* sites. Its demography and population biology in the North Central U.S. have been documented in thorough studies by Werner and Caswell (Werner 1975; Werner & Caswell 1977). Teasel is a large biennial, typically forming dense stands of rosettes and flowering plants with accumulating dried stalks of previous years' plants. Like many biennials, the species is often observed to reach high densities in a site and then decline, with the later possibility of a return to high density when conditions allow (see Van der Meijden et al. 1992). Dense monospecific stands of teasel observed elsewhere suggest that its establishment within populations of *Cirsium vinaceum* might have serious consequences for the persistence of the thistle.

In 1989, we initiated a study of the potential for interference between these two species. Data from 1989–1993 document the spread and increase of teasel in *Cirsium vinaceum* habitats and the potential for direct interactions between the two species. We assessed the possible consequences of teasel invasion by looking at (1) overlap in habitat requirements, reflected in current habitat distribution of the two; (2) similarities of germination requirements and other features of the demography of the two plants; and (3) the outcome of direct competition between the two in field and greenhouse experiments.

Methods

Documentation of Teasel Invasion and Encroachment

We used three approaches to document the encroachment of teasel in habitats supporting *Cirsium vinaceum* (Huenneke et al. 1993). In 1993 we conducted a resurvey of routes covered in a 1990 survey of nonnative weeds in the Lincoln National Forest. The noxious weed survey (Pase & Stockert 1990) was partially updated by driving those routes that had recorded the presence of teasel in the same drainage as *C. vinaceum:* FR (Forest Road) 164, Rio Peñasco; FR 169, Wills Canyon; FR 247, Russia Canyon; FR 460, Scott Able; FR 537, Sacramento River; FR 5009, Water Canyon; and portions of State Road 24. Two additional routes were also surveyed: Trail 9236B, Lucas Canyon; and Trail 5007, Benson Canyon. Both have known populations of *C. vinaceum* and are near drainages with known populations of teasel. Both surveys involved driving or hiking the routes and recording teasel presence along the route by noting the mileage where populations of teasel started and ended. Sampling was done in late May 1993, when teasel rosettes were large enough to spot from the vehicle and nearly all of the previous year's teasel stalks were still standing.

We also resampled transects established in 1989 in *Cirsium vinaceum* populations where teasel had appeared. Seven permanent transects were established by the Lincoln National Forest in 1989 through areas with adjacent or co-occurring teasel and *C. vinaceum.* Line-intercept data (extent and location of patches of the two species) were recorded then and again by us in 1993.

Finally, we surveyed quadrats in mixed populations in 1993 to determine whether the two species actually come in contact with one another. Individual plants in quadrats were counted and measured to determine whether teasel seedlings occur within patches of thistle and whether small plants of either species are affected by the presence of the other. Transects were laid out through mixed populations, and 1-m^2 quadrats were marked out every 4 meters (number of quadrats varied with the width of the population). We sampled Scott Able Canyon, the Water Canyon exclosure, West Bluff Springs, and Benson Canyon (all within the Lincoln National Forest).

Habitat Requirements

During spring and summer of 1989, habitat data were collected at 16 randomly selected *Cirsium vinaceum* sites, 6 teasel sites, and 14 sites occupied by both species (interspersed). Thirty thistle populations were randomly selected from the Lincoln National Forest's list of 52 populations; the teasel sites were discrete populations located near thistle sites. Those thistle populations that had both species growing together constituted the sample of interspersed populations.

At each site, at least 10 1-m^2 quadrats were established, and the following data were recorded for each quadrat: number and percentage cover of thistle rosettes and seedlings, number and percentage cover of teasel rosettes and seedlings, soil surface pH, aspect, slope, distance to road, distance to open water, percentage total cover of vegetation, percentage cover of other dicots, percentage cover of grass. Mean values of each variable per site were calculated and used in analyses of variance to assess significance of differences among types of sites. Contingency tables (2×2) and Fisher's exact test were used to examine possible associations between occurrences of the two plant species and the presence of roads.

Germination Responses

Seed germination is a critical stage in the life history of most plants and in the determination of community dominants and succession in many ecosystems. We compared the germination responses of *Cirsium vinaceum* and *Dipsacus sylvestris* in the laboratory to gain insights into the possible outcomes when seeds of both species are present. Mature seed heads of both species were collected from the Lincoln National Forest in August 1989; *Cirsium vinaceum* was collected from Scott Able Canyon, and teasel was collected from the Cox–

Rio Peñasco population. Achenes from the thistle, hereafter called seeds, were removed from the seed heads, inspected, and counted. Only filled, light-colored seeds with no evidence of larval insect attack or infection were used in the germination trials. Seeds were stored under refrigeration for approximately five months until experiments were initiated. Although germination trials in the field would have been preferable, these could not be performed in the protected thistle populations.

After treatment with 5% bleach to discourage fungal infection, seeds were placed on filter paper moistened with distilled water in Petri dishes. The four treatments were (1) dark (dish wrapped in foil) at room temperature (measured at 22° C); (2) dark at 10° C; (3) dark at 30° C; (4) light (9 hours light, 15 hours dark) at room temperature. Each treatment was applied to five replicates of each species, and each replicate was a dish containing 10 seeds (from 10 different seed parents). Thus, 200 seeds were used for each species. Dishes were checked daily, water was added as necessary, and germinations (piercing of seed coat and extension of radicle) were recorded. To assess overall viability, 60 seeds of each species were tested with 2,3,5-triphenyl tetrazolium chloride (Bradbeer 1988). A two-factor analysis of variance was used to assess differences among species and treatments.

Demographic Comparisons

Demographic study of a population can reveal its current rate of growth, the causes and rates of mortality of individuals, and the sensitivity of the plant's life history to environmental fluctuation. Population models have been developed to summarize the demography of teasel elsewhere (Werner & Caswell 1977), and the similarity of the life history of these two robust rosette species suggested that it would be straightforward to construct population models to compare their behavior in the Lincoln National Forest.

Four populations of *Cirsium vinaceum* were selected randomly from a list of 40 that the Lincoln National Forest determined suitable for sampling (large, isolated from heavy recreational use). Sites were selected to represent both grazed and ungrazed (no domestic livestock) conditions and both spring and stream habitat. One fenced spring population (Water Canyon #4), one unenclosed spring population (Water #7), one fenced stream population (Silver Springs), and one unenclosed stream population (Scott Able) were selected. Concerns of the U.S. Forest Service about limiting access to *C. vinaceum* populations prevented us from replicating these site types. One population of *Dipsacus sylvestris,* in similar streamside habitat within a drainage supporting the thistle (Cox–Rio Peñasco), was also selected for sampling. Within each population, approximately 10 1-m^2 quadrats were established, and all individual plants in each quadrat were tagged with plastic markers placed at the base. Total sample size initially was at least 200 plants per population. Each plant was visited and monitored several times between June 1989 and September 1989. Quadrats were revisited in May 1990 to assess overwintering changes and in August 1990 to give estimates of rate of change in a year's interval. At each visit plants were recorded as being in one of 6 categories: (1) seedling; (2) rosette diameter between 4.5 and 30 cm; (3) rosette diameter between 30 and 70 cm; (4) rosette diameter more than 70 cm; (5) flowering stem; and (6) dead.

Rates of change of individuals from one category to another were calculated over the one-year-interval. Rates were used to construct transition matrix models (Caswell 1989) summarizing the rate of current population growth for each of the one teasel and four thistle populations.

Competition Experiments

There is a tremendous literature documenting the effects of competition among neighboring plants, within and among species (see recent syntheses by Grace & Tilman 1990; Keddy 1989). This competition is probably better termed interference, because there may be other mechanisms operating instead of or in addition to simple competition for a tangible resource such as water or nitrogen. Plant ecologists and agronomists have long used experimental methods to measure the strength of this interference and to predict the outcome of competition in cases where individuals of two species are growing interspersed. We carried out experiments in both field and greenhouse, in which individuals of *C. vinaceum* and *D. sylvestris* were grown in deWit replacement series (deWit 1960; Harper 1977), to gain insight into the potential effects of teasel on individual thistle plants. Simple deWit designs are not entirely satisfactory because they do not adequately assess the role of density, and results can be strongly influenced by specific conditions such as pot size or shape. Herben and Krahulec (1990) and Snaydon (1991), among others, offer criticisms and improvements on this approach. But the constraints of working with a protected species led to some compromises in the design and execution of these experiments because of severe restrictions on the number of seeds to be collected and the manipulations allowed in the field.

In the greenhouse, seedlings derived from germinants in the seed germination trials were planted in 5-gallon (roughly 23-liter) pots in a commercial potting soil. In a deWit replacement series, total plant density (number of plants per pot) is kept constant and the ratio of numbers of the two competing species is varied. Thus, the effects of an individual competitor—in this case, teasel—can be assessed relative to the effects of an individual of the target species—the thistle. Four plants were grown in each pot. Treatments were as follows: 4 *Cirsium*, 0 *Dipsacus*; 3 *C.*, 1 *D.*; 2*C.*, 2 *D.*; 1 *C.*, 3 *D.*; and 0 *C.*, 4 *D.* (five treatments). There were four replicates of each treatment. Pots were interspersed on the greenhouse bench, watered daily with a drip irrigation system, and fertilized monthly during the growth period (98 days, June 27–October 3, 1990). Leaf number and rosette diameter were recorded for individual plants at the initiation and conclusion of the growth period. Rosette growth (change in diameter), averaged for individuals of a species within a pot, was used as the variable to assess performance. Restrictions on the number of thistle seeds collected prevented us from repeating the experiment for other densities or pot sizes. Requirements to maintain all living thistles intact at the end of the experiment prevented us from using biomass as a measure of plant growth or performance.

A similar experiment was initiated in the field in a Rio Peñasco population 0.5 km west of Bluff Springs, where the two species were growing interspersed. In July 1989, 0.25-m^2 quadrats (50 cm × 50 cm) were selected nonrandomly to contain the desired number of *C. vinaceum* individuals and the desired number or more of teasel. Teasel individuals were thinned if necessary to reach the desired number (for totals of either four or eight plants per quadrat). Because thistle density varied and because thistles could not be removed or transplanted, we were forced to use quadrats with varying initial plant density (and probably environmental conditions). The same constraints prevented us from using other, better designs for evaluating competition in the field (for example, the method of Goldberg & Werner 1983). Eight replicate quadrats of each of five treatments were established: 100% *Cirsium*; 75% *C.*, 25% *D.*; 50% *C.*, 50% *D.*; 25% *C.*, 75% *D.*; and 100% *D.* Individual quadrats contained 4–8 plants total, depending on the number of *Cirsium* within the quadrat, the relative densities of the two species, and the particular ratios needed. Treatments were interspersed as much as possible in the population, and both high- and low-density quadrats were represented within each treatment. All individuals of both species in the quadrats were tagged with plastic stakes. Maximum rosette diameter was measured for each individual, and the plants were placed into one of the six categories used in the demographic study. After one year of growth, plants were recensused in August 1990 to determine changes in plant size and status.

Results and Discussion

Documentation of Teasel Invasion and Increase

The resurvey of the noxious weed survey routes documented an increase in both the number and extent of teasel populations in drainages occupied by *C. vinaceum* (Table 1). Although most biennials behave like transient or fugitive species, with local populations appearing and disappearing over short time periods as conditions change (Van der Meijden et al. 1992), there were no cases where a stand observed in 1990 was not observed as still present in 1993. In essentially every case, the density and the spatial extent of the teasel population had increased over that time period. In three of the five resurveyed routes, the number of discrete occurrences had increased. Thus, known occurrences of teasel in *C. vinaceum* habitat have increased over the past three years. The presence of both rosettes and flowering stalks confirms that the invader is reproducing in each of these sites.

In the seven permanent transects, abundance of *C. vinaceum* differed between 1989 and 1993 in individual transects, but, when data from all seven are summed, there was essentially no net change in the cover of the thistle (net sum of changes, 1% increase for all seven transects summed). Many individual transects showed changes in the percentage cover of teasel, but the three transects with large increases in teasel outweighed the decreases in the others. In one case there was a substantial increase of teasel (21% to 42%, line intercept) and a decline in thistle cover (13% to 5%). Other increases in teasel were accompanied by increases in thistle, suggesting that all vegetative cover might have been higher overall in the second sampling. Points of contact between the two species increased on two transects. A decrease in points of contact between the two on one transect resulted from the disappearance of thistle from a portion of the transect. Thus, the opportunities for the two species to grow side by side do appear to be increasing in at least some sites.

The quadrats in mixed populations demonstrated that the two species can indeed intermingle. Roughly 20% of the sampled quadrats contained both species in a single square meter. Of the 57 total quadrats, six contained seedling *Dipsacus* in proximity to large thistles and six contained seedling *Cirsium* in proximity to large teasel. It seems, then, that seedling recruitment sites are similar for the two species. We observed 14 thistle individuals whose nearest neighbors were large teasel. We revisited

Table 1. Summary of changes noted in resurvey of routes with both teasel and *Cirsium vinaceum* from 1990 noxious weed survey (Pase & Stockert 1990).

	Total Mileage Occupied		*Number of Occurrences*	
Route	*1990*	*1993*	*1990*	*1993*
FR 537	1.6 miles	1.8 miles	2	4
FR 460	0.1 miles	0.4 miles	1	1
FR 164	10.0 miles	10.9 miles	2	2
FR 169	2.9 miles	4.1 miles	6	8
T 5005	(not surveyed)	0.5 miles	(ns)	1
T 5009	1.1 miles	1.5 miles	3	6

two of these sites in late summer and noted substantial additional recruitment of seedlings, particularly for teasel. In a number of quadrats, teasel seedling density exceeded 150 seedlings per square meter. Thistle seedling density, on the other hand, did not exceed 20 seedlings per square meter.

In summary, teasel shows the ability to establish as seedlings at high density within *Cirsium vinaceum* populations. In addition, over the past 3–4 years, the number of occurrences of teasel has been increasing within thistle habitat. The two species do co-occur and intermingle, at least in some portions of their habitat ranges.

Habitat Requirements

Habitat for these species in the Sacramento Mountains comprises streamsides, springs, and seeps with a dense herbaceous layer but no tree canopy. There were no significant differences among the three types of populations in slope, aspect, distance to water, or variables related to plant cover (ANOVAs for each variable, $p > 0.05$). Soil surface pH did vary significantly ($p < 0.05$) but only slightly; mean pH averaged 8.1 for thistle and interspersed sites but was 7.5 for teasel sites. Given the small difference in values and the large number of significance tests performed, it is unlikely that this difference represents any meaningful difference in species' habitat requirements. The thistle is restricted in its distribution to specific habitats (travertine springs and water courses influenced by them [Thomson 1991]), but teasel has quite a broad distribution throughout North America, suggesting a wide habitat breadth. All observed teasel populations (19 of 19) were adjacent to roads, but *Cirsium* distribution was independent of roads (Fisher's exact test, $p < 0.0001$ for teasel, $p = 0.772$ for *Cirsium*). Initial establishment of teasel may thus depend on human disturbance to create dispersal routes. However, similarity of site characteristics in the Lincoln National Forest, and the presence of interspersed populations, both confirm that teasel is capable of establishment and growth in *Cirsium vinaceum* habitat.

Germination Responses

The two species demonstrated roughly similar germination behavior; a two-factor ANOVA found no significant difference among species (species factor, $F_{1,32} = 0.733$, $p = 0.407$). Treatments did differ ($F_{3,32} = 12.510, p < 0.001$); germination was highest in the light at room temperature (54% germination for each species). This represented essentially all viable seeds (assessment of viability with tetrazolium was 42% for the thistle, 53% for teasel). *Cirsium vinaceum* germination was significantly higher in the light than in the dark (28%) at room temperature, but teasel showed no significant difference in germination between light and dark at room temperature. Both species germinated only poorly at other temperatures (Fig. 1). When water, soil, and temperature conditions in the field are adequate, both species would apparently be able to respond. Teasel, however, demonstrated superior ability to germinate in the dark. This is important in relation to the often-noted inability of thistles to germinate when light is limited (Pons 1983; Wilson & McCarty 1984; Mitchell & Woodward 1988), a characteristic that ensures that most thistles can establish as seedlings only in open conditions. *Cirsium vinaceum* appears to share this trait. Given the dense, leafy stands characterizing *Cirsium vinaceum* populations and the extremely dense canopies formed by teasel where it has invaded successfully, *Dipsacus* would be predicted to experience higher germination success than *C. vinaceum* where the two species are growing interspersed.

Demographic Comparisons

During summer 1989, 10–35% of the rosettes in the thistle populations produced flowering stems. Seedling numbers were fairly high (8–50% of total individuals). Approximately 12% of the total individuals died over the course of the year. More than three quarters of the deaths were over the winter, and of course flowering stems (which die after reproduction) contributed many of these. Seedlings also experienced substantial mortality.

In the single year of study, net population growth ranged from rapid decline (Silver Springs, R_0 or replace-

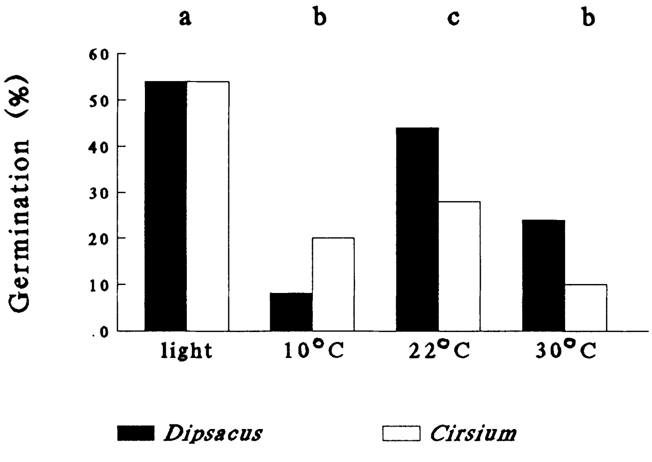

Figure 1. Mean germination for Dipsacus sylvestris *and* Cirsium vinaceum *in Petri-dish trials. Conditions were 22° C with light (9 hours light/15 hours dark), 10° C dark, 22° C dark, 30° C dark. Species did not differ significantly; different letters above bars indicate treatments that differ significantly (95% LSD).*

ment rate = 0.7456) to rapid increase (Water #4, R_o = 1.379). Replacement rate was for 1.0123 for Water #7 and 0.9059 for Scott Able. The teasel population experienced a slight decrease in size (R_o = 0.9739). These rates should not be interpreted as predictions of the fate of individual populations because fluctuations in weather and other conditions between years typically cause extreme fluctuations in demographic rates over the short term. They demonstrate, however, that in a given year teasel population behavior can be within the same range as that of individual *Cirsium* populations. Rates of growth of seedlings and small rosettes into larger size classes appeared to be more rapid in teasel than in the thistle. Observations in the 1993 seedling quadrats also found much higher plant densities for teasel than for thistle in those sites where the two grow interspersed.

Greenhouse and Field Competition Experiments

In the greenhouse experiment, plant sizes of the two species were equivalent: mean rosette size for *C. vinaceum* was 38.8 cm and *D. sylvestris* averaged 38.6. The presence of teasel within a pot had a strong negative effect on the performance of individual thistles, with thistles in the 1 *C.*, 3 *D.* treatment displaying growth significantly lower than that in the 4 *C.*, 0 *D.* pots (ANOVA, $F_{3,12}$ = 4.797, p = 0.020; Fig. 2). Teasel, on the other hand, showed no response to the presence of the thistle. Individual teasel plants showed equal growth rates regardless of treatment ($F_{3,12}$ = 0.352, p = 0.789). In addition, three thistles died during the latter half of the growth period, and teasel experienced zero mortality. The outcome of greenhouse competition experiments is notoriously dependent on the particular conditions of the trial; results may change with the size of pot used, nutrient availability, and so on. Thus we cannot be confident that the degree of growth suppression experienced by *Cirsium vinaceum* in this experiment would be observed under field conditions. But the study does demonstrate the potential for negative effects on the thistle when seedlings of the two species are growing in close proximity.

During the one year of observation in the field experiment, density had no significant effect on the fates of individual plants. There were no significant differences in demographic fate (growth, mortality, etc.) among treatments for thistle individuals. Average rosette growth was slightly lower (but nonsignificantly so) in quadrats with higher percentages of teasel present (Fig. 2; ANOVA, $p > 0.20$). In contrast, teasel showed significantly lower growth rates when growing as a minority component ($F_{3,28}$ = 3.262, p = 0.036); in fact, several teasel rosettes in the 75% *C.*, 25% *T.* treatment died

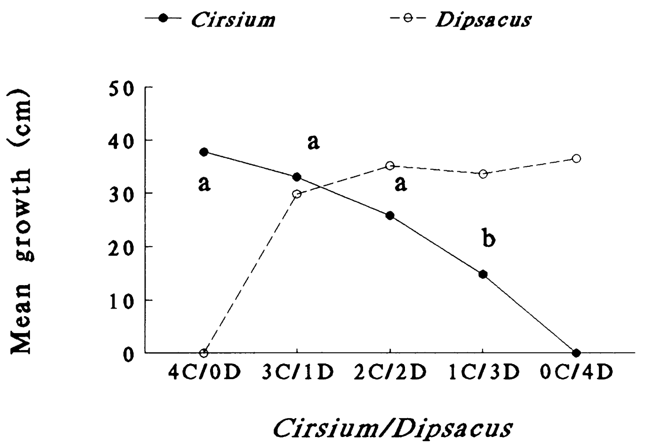

Figure 2. Mean growth of rosettes of Cirsium vinaceum *and* Dipsacus sylvestris *in a greenhouse replacement series experiment. Ratios of the two species range from four* Cirsium *and no* Dipsacus *(4C/0D) per pot to no* Cirsium *and four* Dipsacus *per pot (0C/4D). Values plotted are average growth of rosettes (diameter, in cm) in a treatment. Different letters near* Cirsium *points indicate significantly different mean growth rates (according to 95% LSD);* Dipsacus *growth rates did not differ significantly among treatments.*

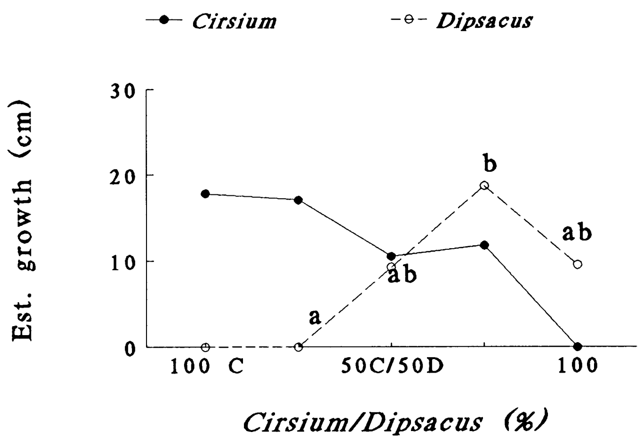

Figure 3. Mean estimated (Est.) growth of rosettes (diameter, in cm) for Cirsium vinaceum *and* Dipsacus sylvestris *in a field replacement series experiment. Ratios of the two species range from 100%* Cirsium *(100C) per quadrat, through 75%* Cirsium/*25%* Dipsacus, *50% of each species, 25%* Cirsium/*75%* Dipsacus, *to 100%* Dipsacus *(100D) per quadrat. Different letters near* Dipsacus *points indicate significantly different mean growth rates (according to 95% LSD);* Cirsium *growth rates did not differ significantly among treatments.*

over the observation period. The results of the field experiment are inconclusive given the small degree of replication and the problems controlling for environmental variation that probably exists among plots with different initial densities of *Cirsium vinaceum*. Overall, density was somewhat lower than in the greenhouse pot experiment.

Conclusions

There appears to be substantial potential for interference effects of teasel on the threatened *Cirsium vinaceum*. Descriptions of the habitat distributions of the two species in the Lincoln National Forest suggest similar responses to environment, although teasel is associated currently with roads at this early stage in its invasion of the Sacramento Mountains. The germination responses of the two species are roughly equivalent, although teasel may be better able to germinate under conditions of crowding or competition. There are few differences in the demographic patterns of the two over the short time span studied, with both capable of rapid growth through the rosette stage. Direct evidence of interference in experimental studies suggests that under at least some environmental conditions teasel seedlings and rosettes may have a negative effect on the growth of similarly sized thistles. While teasel performance may be poor in dense thistle stands, observations suggest that teasel may increase its representation in sites currently dominated by *Cirsium vinaceum* and that the thistle may experience difficulty in maintaining high rates of growth and seedling recruitment once the two species are growing interspersed.

Detailed studies of the possible interactions between two species require substantial effort and time. We suggest that such investigation be undertaken only when the potential for impact on a sensitive species seems greatest. That is, concern should be triggered when a weed known to be invasive in natural ecosystems elsewhere becomes established in the vicinity of a sensitive plant species; when the sensitive species is found in a habitat known to be vulnerable to biological invasions, such as islands and riparian systems (Mooney & Drake 1986); and when the weed appears to be adapted to the natural disturbance regime or to anthropogenic disturbance recently introduced to the ecosystem (Hobbs & Huenneke 1992). If at least one of these danger signals is present, some investigation of the biology of interactions between invader and sensitive species is warranted.

What areas of research will be most productive? Habitat descriptions can be time-consuming and may not be particularly informative, especially when the invasion is in its earliest stages and current distribution may not reflect the nonnative plant's ability to succeed in various kinds of sites. Similarly, demographic study may require too much time and effort for the information it yields; variability among years and sites means that conclusions about the relative performance of the two species will be weak.

Studies of germination behavior are relatively quick and inexpensive, and they produce data directly relevant to an assessment of the relative abilities of the two species to establish from seed when growing together. Experimental conditions should be relevant to field conditions. Important variables of seed germination response to be measured might include dependence on light or dark, requirement for scarification or other pretreatment, total germination, and rate or speed of germination.

Experimental studies of competition appear to provide direct evidence of the potential for interference. Care must be taken, however, because of the sensitivity of the outcome to initial conditions (Firbank & Watkinson 1990). Greenhouse or garden experiments are useful but ideally should be repeated using several different growing conditions to test the generality of the results. Unfortunately, such repeated experiments are difficult when plant material is hard to obtain or when experimental populations cannot be established easily. Field experiments are also difficult when one species cannot be manipulated because there are almost certainly initial differences between plots with high densities and those with low densities of the sensitive species, and those differences may confound the results of the actual species interactions.

Our experiences with *Cirsium vinaceum* reflect a problem of the sort that affects any proposal to investigate the biology of a rare, protected species. The collection of seeds or plants to work with, the manipulation of plants or of environment in the field, and the destructive sampling necessitated by many sorts of biological study all pose constraints—logistical and ethical—on the study of rare plants (Huenneke 1995). Small sample sizes and limitations on manipulations or experimentation can make it difficult to execute well-designed studies yielding insight into the ecology and the management of those species. It is essential that compromises be forged among permit-granting agencies, managers, and researchers to provide the most useful information possible with the least risk to the conservation target.

Any natural area or reserve is being bombarded continually with potential invaders. Ecologists and managers are interested in developing the ability to forecast success or failure of a specific introduction (Crawley 1989; Pimm 1989) before the invasion has proceeded too far. Only by accurately identifying those invaders most likely to pose threats to a rare species will they be able to allocate resources effectively to control of the invader and to efforts on behalf of the sensitive native species.

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